

WHEN CORRELATIONS MATTER - RESPONSE OF DYNAMICAL NETWORKS TO SMALL PERTURBATIONS

Thimo Rohlf^{1,2}, Natali Gulbahce^{3,4} and Christof Teuscher⁵

¹Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

²Max-Planck-Institute for Mathematics in the Sciences, Inselstrasse 22, D-04103 Leipzig, Germany

³Center for Complex Network Research, Northeastern University, Boston, MA 02115, USA

⁴Center for Cancer Systems Biology, Dana Farber Cancer Institute, Boston, MA, 02215, USA

⁵Los Alamos National Laboratory, CCS-3, MS B256, Los Alamos, NM 87545, USA
rohlf@santafe.edu

ABSTRACT

We systematically study and compare damage spreading for random Boolean and threshold networks under small external perturbations (damage), a problem which is relevant to many biological networks. We identify a new characteristic connectivity K_s , at which the average number of damaged nodes after a large number of dynamical updates is independent of the total number of nodes N . We estimate the critical connectivity for finite N and show that it systematically deviates from the annealed approximation. Extending the approach followed in a previous study [11], we present new results indicating that internal dynamical correlations tend to increase not only the probability for small, but also for very large damage events, leading to a broad, fat-tailed distribution of damage sizes. These findings indicate that the descriptive and predictive value of averaged order parameters for finite size networks - even for biologically highly relevant sizes up to several thousand nodes - is limited.

1. INTRODUCTION

Random Boolean networks (RBN) were originally introduced as simplified models of gene regulation [5, 6]. In the limit of large system sizes, they exhibit a dynamical order-disorder transition at a critical wiring density K_c [4]; similar observations were made for sparsely connected random threshold (neural) networks (RTN) [7, 10]. For a finite system size N , the dynamics of both systems converge to periodic attractors after a finite number of updates. At K_c , the phase space structure in terms of attractor periods [1], the number of different attractors [13] and the distribution of basins of attraction [2] is complex. Furthermore, critical networks exhibit many properties reminiscent of biological networks, leading to the idea K_c might be an "attractor of evolution" [6].

To ensure proper function, regulatory networks in living cells have to be robust (insensitive) against external perturbations. In terms of RBN/RTN dynamics, perturbations can disrupt the generic dynamical state (fixed point or periodic attractor) of the network, and hence are referred to as "damage"; this type of study has been applied,

for example, to the perturbation of gene expression patterns in a cell due to mutations [9].

Mean-field techniques as, for example, the *annealed approximation* (AA) introduced by Derrida and Pomeau [4], allow for an analytical treatment of damage spreading and exact determination of the critical connectivity K_c under various constraints [14]. It has been shown that local rewiring rules coupled to mean-field-like order parameters of the dynamics can drive both RBN and RTN to self-organized criticality [3, 8].

Studies of RBN/RTN dynamics based on the AA usually implicitly assume that, at least for large N , *principal* properties of damage spreading should not depend on the initial perturbation size. For example, the determination of K_c using a one-bit initial perturbation (sparse percolation limit), or an initial perturbation size increasing with N should yield the same value for large N , since it is assumed that correlations can be neglected in this limit by averaging over a large number of different random network realizations. In this paper, we extend results of a previous study [11] and present the following findings that are, at least in part, in clear contradiction to these assumptions:

- In section 3.1, we identify a new characteristic point $K_s < K_c$, where the expectation value of the number of damaged nodes after large number of dynamical updates is independent of N .
- By the definition of marginal damage spreading, we estimate the critical connectivity $K_c(N)$ for finite N , and present evidence that, even in the large N limit, for small initial perturbations K_c systematically deviates from the predictions of the AA (section 3.2).
- In section 3.3, we present new results proving that, slightly below K_c , starting from random initial conditions, the AA holds only for small times t , indicating that after passing transient dynamics inherent correlations considerably affect damage propagation.

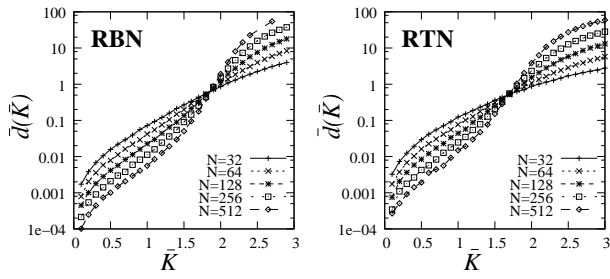


Figure 1. Average Hamming distance (damage) \bar{d} after 200 system updates, averaged over 10000 randomly generated networks for each value of \bar{K} , with 100 different random initial conditions and one-bit perturbed neighbor configurations for each network. For both RBN and RTN, all curves for different N approximately intersect in a characteristic point K_s .

- Last, we show that vanishing, as well as large damage events are overrepresented in damage size statistics, leading to highly skewed distributions, which are poorly characterized by averages (section 3.4).

2. DYNAMICS

2.1. Random Boolean Networks

A RBN is a discrete dynamical system composed of N automata. Each automaton is a Boolean variable with two possible states: $\{0, 1\}$, and the dynamics is such that

$$\mathbf{F} : \{0, 1\}^N \mapsto \{0, 1\}^N, \quad (1)$$

where $\mathbf{F} = (f_1, \dots, f_i, \dots, f_N)$, and each f_i is represented by a look-up table of K_i inputs randomly chosen from the set of N automata. Initially, K_i neighbors and a look-table are assigned to each automaton at random.

An automaton state $\sigma_i^t \in \{0, 1\}$ is updated using its corresponding Boolean function:

$$\sigma_i^{t+1} = f_i(\sigma_{i_1}^t, \sigma_{i_2}^t, \dots, \sigma_{i_{K_i}}^t). \quad (2)$$

We randomly initialize the states of the automata (initial condition of the RBN). The automata are updated synchronously using their corresponding Boolean functions.

2.2. Random Threshold Networks

An RTN consists of N randomly interconnected binary sites (spins) with states $\sigma_i = \pm 1$. For each site i , its state at time $t + 1$ is a function of the inputs it receives from other spins at time t :

$$\sigma_i(t + 1) = \text{sgn} \left(\sum_{j=1}^N c_{ij} \sigma_j(t) + h. \right) \quad (3)$$

The N network sites are updated synchronously. In the following discussion the threshold parameter h is set to zero. The interaction weights c_{ij} take discrete values $c_{ij} = +1$ or -1 with equal probability. If i does not receive signals from j , one has $c_{ij} = 0$.

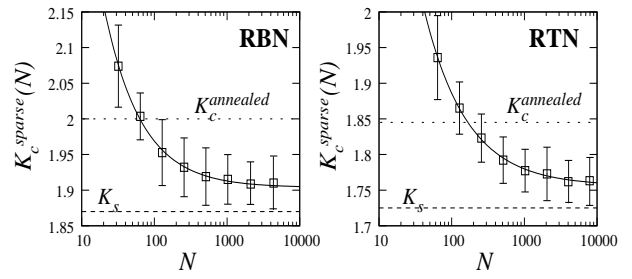


Figure 2. The critical connectivity $K_c^{\text{sparse}}(N)$ in the SP limit as a function of N . Curves are power-law fits according to Eq. (9), straight dashed lines mark K_c^{annealed} and K_s for RBN and RTN, respectively.

3. RESULTS

3.1. Scaling

We first study the expectation value \bar{d} of damage, quantified by the Hamming distance of two different system configurations, after a large number T of system updates. Fig. 1 shows \bar{d} as a function of the average connectivity \bar{K} for different network sizes N by using a random ensemble for statistics. For both RBN and RTN, the observed functional behavior strongly suggests that the curves approximately intersect at a common point (K_s, d_s) , where the observed Hamming distance for large t is independent of the system size N .

We verified this finding quantitatively by using finite-size-scaling methods [11]. In particular, one can show that \bar{d} as a function of N and \bar{K} obeys the following scaling ansatz:

$$\bar{d}(\bar{K}, N) = a(\bar{K}) \cdot N^{\gamma(\bar{K})} + d_0(\bar{K}), \quad -1 \leq \gamma \leq 1. \quad (4)$$

It is straight-forward to show that $\gamma \rightarrow -1$ for small $\bar{K} \rightarrow 0$, and that $\gamma \rightarrow 1$ for densely connected networks above the percolation transition ($\bar{K} > K_c$). Evidently, this implies that at some characteristic connectivity K_s , there has to be a transition from negative to positive γ values, with $\gamma(K_s) \approx 0$. It is a very interesting question whether K_s coincides with K_c , or if it is different from K_c for large N . For a precise numerical determination of K_s , one can make use of the fact that \bar{d} exhibits an exponential dependence near K_c :

$$\bar{d}(\bar{K}, N) \approx c_1(N) \exp[c_2(N) N^\alpha \bar{K}] \quad (5)$$

with $\alpha \approx 0.42$. High-accuracy fits of this dependence (with c_1 and c_2 as adjustable parameters) in the interval $1.6 \leq \bar{K} \leq 2.1$ yield

$$(K_s^{\text{RBN}}, d_s^{\text{RBN}}) = (1.875 \pm 0.05, 0.62 \pm 0.05) \quad (6)$$

for RBN and, correspondingly,

$$(K_s^{\text{RTN}}, d_s^{\text{RTN}}) = (1.729 \pm 0.045, 0.51 \pm 0.04) \quad (7)$$

for RTN. We verified these findings up to $N = 16384$, waiting $T = 5000$ updates for the dynamics to relax; for even larger N , simulations become intractable due to

exponentially increasing relaxation times. Evidently, we tend to miss large damage events since they need the most time to develop. Facing this unavoidable *biased under-sampling* of large avalanches, one can argue that the *true* values of K_s are probably even lower than our measured values. From this evidence, and also from more refined scaling arguments [11], we conclude that K_s is distinct from K_c in the limit of large N .

3.2. Deviations of K_c from the annealed approximation

Interestingly, K_s is close to, but distinct from the critical connectivities $K_c^{RBN} = 2$ and $K_c^{RTN} = 1.845$, as predicted by the AA. Since in this study we consider the limit of very weak initial perturbations which is usually not covered in theoretical studies of RBN/RTN dynamics, we now have to consider the possibility that K_c itself may deviate from the prediction of the AA. An intuitive definition of criticality for finite N can be formulated in terms of *marginal damage spreading*. If at time t one bit is flipped, one requires at time $t + 1$ [14, 10]

$$\bar{d}(t+1) = \langle p_s \rangle(K_c) K_c = 1, \quad (8)$$

where $\langle p_s \rangle(\bar{K})$ is the average damage propagation probability. Fig. 2 shows $K_c^{sparse}(N)$, using the values $c_1(N)$ and $c_2(N)$ obtained from numerical fits of Eq. (5) for both RBN and RTN. We find that both systems, in a very good approximation, obey the scaling relationship

$$K_c^{sparse}(N) \approx b \cdot N^{-\delta} + K_c^\infty \quad (9)$$

with $b = 3.27 \pm 0.79$, $\delta = 0.85 \pm 0.07$ and $K_c^\infty = 1.9082 \pm 0.008$ for RBN and $b = 3.853 \pm 0.76$, $\delta = 0.736 \pm 0.05$ and $K_c^\infty = 1.7595 \pm 0.008$ for RTN. Hence, in the limit $N \rightarrow \infty$, we can extrapolate

$$K_c^{\infty, RBN} = 1.9082 \pm 0.008 \quad (10)$$

for RBN, and for RTN

$$K_c^{\infty, RTN} = 1.7595 \pm 0.008. \quad (11)$$

Thus, for both RBN and RTN in the sparse percolation limit, we make the surprising observation that K_c^{sparse} systematically deviates from $K_c^{annealed}$. While we find $K_c^{sparse}(N) > K_c^{annealed}$ for small $N < 128$, for larger N we observe a monotonic decay that approaches an asymptotic value considerably below $K_c^{annealed}$, suggesting that the observed deviations from the AA also hold in the large N limit. In the following two subsections, we will extend this analysis and discuss possible causes for these deviations.

3.3. Time dependence of \bar{d}

Since we found systematic deviations from the AA for large t , it is interesting to ask whether the AA still holds for small t , starting from random initial states. In particular, one can derive the following recursive map for damage propagation at $t > 0$ [10]:

$$\bar{d}(t) = N \cdot \langle p_s \rangle(\bar{K}) \cdot \left(1 - e^{-\bar{K} \cdot \bar{d}(t-1)/N}\right), \quad (12)$$

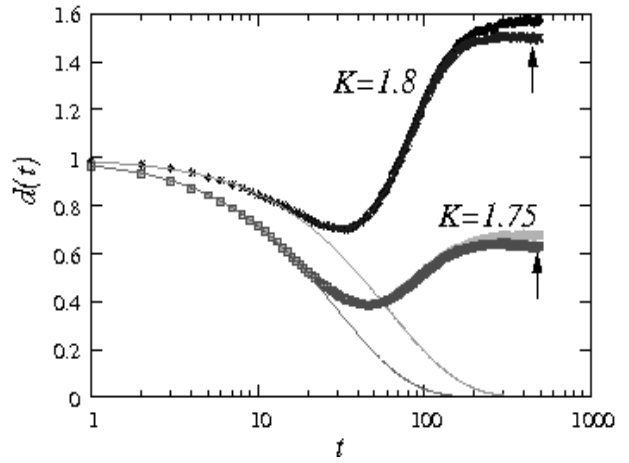


Figure 3. Time-dependence of (average) damage propagation in RTN of size $N = 4096$ just below K_c ; damage \bar{d} at time t was averaged over 10^5 network realizations and 100 different initial conditions (and the corresponding neighbor states with one bit perturbed at random) at $t = 0$ for each data point. Lined curves are the corresponding solutions of the AA (Eq. (12)). For $t \geq 20$, pronounced deviations of simulation results from the AA are found, in particular for $\bar{K} = 1.8$. Arrows indicate results with "corrected" statistics, i.e. without "pseudo-damage" due to attractor phase lags.

where $\langle p_s \rangle(\bar{K})$ is the average probability that a link propagates damage. Let us now test this relationship in the interesting range $K_s \leq \bar{K} \leq K_c^{annealed}$ for ensembles of randomly generated networks (RTN with Poissonian degree-distribution), with one-bit perturbations of randomly chosen initial conditions. Figure 3 shows that, for small t , the dependence for $\bar{d}(t)$ found in numerical simulations obeys this prediction very well. However, after an initial decrease of $\bar{d}(t)$, an *increase* above the initial damage size (i.e. supercritical behavior) is found, in clear contradiction to the AA. This indicates that, after the system has passed transient dynamics, inherent dynamical correlations considerably modify damage propagation (fractal structure of attraction basins [2]). One can also show that "pseudo-damage" events, i.e. cases where networks run on the same attractor, but with a phase lag captured in a non-zero Hamming distance, do *not* substantially contribute to this effect (arrows in Fig. 3). This proves that our results are very robust against changes in the way statistics is taken.

3.4. Distribution of damage sizes

Let us now go beyond averaged (mean-field) quantities and investigate detailed statistics of damage sizes. For this purpose, for different \bar{K} and N ensembles of Z_e random network realizations were created; for each network realization, Z_i random initial conditions $\vec{\sigma}$ (plus a neighbor state with one bit perturbed at random) were tested, and statistics of damage sizes was taken after 1000 dynamical updates. Notice that we do *not* average damage sizes for a given network realization, since this would again represent a kind of mean-field approximation. Figure 4 shows that the resulting statistical distributions near K_c

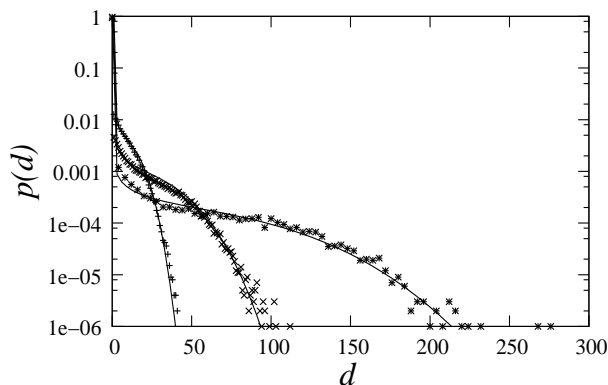


Figure 4. Statistical distribution $p(d)$ of damage sizes for three different system sizes: $N = 64$ (+), $N = 256$ (x) and $N = 1024$ (*). Lined curves are solutions of Eq. (13).

are highly skewed, with more than 90% events of vanishing damage size, and a flat tail of large damage events which becomes more and more pronounced for increasing N . Similar problems have been studied by Samuelsson and Socolar [12] for the number of *undamaged* nodes u in the limit of *exhaustive* percolation. From symmetry considerations, it follows that the probability distribution $p(d)$ of the number d of *damaged* nodes in the limit of sparse percolation obeys a similar dependence as u in the case of exhaustive percolation, and hence

$$p(d) \approx a(N) \cdot \frac{\exp[-\frac{1}{2}(d \cdot N^{-2/3})^3]}{\sqrt{d \cdot N^{-2/3}}}, \quad (13)$$

where $a(N)$ is a free parameter. One finds that the results of numerical simulations agree very well with this estimate even for considerably small N (Fig. 4). From the shape of these distributions, one recognizes that vanishing, as well as large damage events are much more probable than expected from mean-field considerations. In part, this explains the deviations from the annealed approximation found for \bar{d} near criticality (Fig. 3), and it also questions in how far averaged quantities deliver an informative description of RBN/RTN dynamics for finite size N .

4. DISCUSSION

We showed that, for very weak (one-bit) perturbations of the initial states of RBN and RTN dynamics, the resulting damage at later times exhibits a non-trivial scaling with network size N , and, near the critical order-disorder transition - the so-called the 'edge of chaos' - considerable deviations from the annealed approximation. These deviations have escaped earlier studies, since usually the *rescaled* damage \bar{d}/N (or the overlap $1 - \bar{d}/N$, respectively) was studied, and the thermodynamic limit of large N was considered. Our study indicates that there is a strong need for more refined studies of damage propagation in RBN/RTN, that explicitly take into account dynamical correlations and the fractal structure of attraction basins [2]. One may expect that the situation is even more complex for networks with more realistic topologies. Even for simple random graphs, as applied in this

study, damage size distributions are highly skewed, questioning the descriptive and predictive value of simple, averaged order parameters for this class of complex systems.

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